

A NEW SPECIES OF HIGH-ALTITUDE FROG (*ELEUTHERODACTYLUS*: LEPTODACTYLIDAE) FROM THE CORDILLERA ORIENTAL OF COLOMBIA

by

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Resumen

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Se describe *Eleutherodactylus nervicus* del Alto del Tigre, un alto en la limite Cundinamarca y Meta. La especie tiene parentescos con *E. nicefori* pero tiene discos digitales angostos. Se redescubre *E. nicefori* usando muestras mas completas de sus poblaciones. Se encuentra la especie en los páramos en el norte de Boyacá, el sur de Norte de Santander, y el sureste de Santander. *Eleutherodactylus nicefori* es una especie polimorfo en patrones, como muchas especies del género. La especie tiene discos reducidos con poca evidencia de las almohadillas ventrales (sus falanges terminales son parecidas a ellas de las especies del género *Phrynopus*). A pesar de las similitudes superficiales, *E. nervicus* y *E. nicefori* no tienen parentescos con *E. ginesi* de la Cordillera de Mérida en Venezuela.

Abstract

Eleutherodactylus nervicus is described from the Alto del Tigre on the border between Cundinamarca and Meta. The species is closely related to *E. nicefori* but has obvious digital disks. *Eleutherodactylus nicefori* is redescribed based on a more complete sampling of its populations. The species is distributed in páramo habitats in northern Boyacá, southern Norte de Santander, and southeastern Santander. *Eleutherodactylus nicefori* is pattern polymorphic, like many species of the genus, but has reduced digital disks with little evidence of ventral pads (its terminal phalanges approach those of frogs of the genus *Phrynopus*). In spite of superficial similarities, *E. nervicus* and *E. nicefori* are not closely related to *E. ginesi* of the Cordillera de Mérida, Venezuela.

In the course of reviewing uncatalogued material in the amphibian collection of the Instituto de Ciencias Naturales, I found a bottle of small frogs taken from a very high elevation (3870 m) in the Cordillera Oriental. Superficially, they appeared to be *Eleutherodactylus nicefori* Cochran & Goin but this view was revised immediately upon direct comparisons of individuals. However, I needed to review all of the material of *E. nicefori* in the Instituto's collections to convince myself that the frogs from the Alto del Tigre (limite Cundinamarca-Meta) did not represent merely a geographic variant of *E. nicefori*. This provided me the opportunity to review the contention of Lynch (1981a) that *E. nicefori*

was the near relative of *E. ginesi* (Rivero) of the Cordillera de Mérida in Venezuela.

Small high-altitude *Eleutherodactylus* having narrow digits were first reported from eastern Colombia and western Venezuela by Rivero (1964) who named *Eupsophus ginesi*. Lynch (1968) assigned the species to *Eleutherodactylus* following study of a specimen once in the possession of the late Roberto Donoso-Barros. Cochran and Goin (1970) named *Eleutherodactylus nicefori* from the Páramo del Almorzadero in southern Norte de Santander but did not contrast it with *E. ginesi* but rather with *E. curtipes* (Boulenger) of Ecuador. Lynch (1976) placed each species in his *unistrigatus* group. Duellman & Simmons (1977) reported additional material of *E. nicefori* from near the type-locality. Lynch (1979)

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illustrated the skull of *E. nicefori* but made no comment about it. **Lynch & Duellman** (1980) included *E. ginesi* and *E. nicefori* in a "series" (a subset of an "assembly") with the Ecuadorian *E. trepidotus* Lynch. **Lynch** (1981a) included the two species within his *myersi* series.

Rivero (1984) provided much detail about *E. ginesi* and compared it with *E. curtipes* and *E. myersi*. He used the absence of vocal slits as a grouping character (*myersi* + *nicefori* + *ginesi*, noting that vocal slits were absent in *E. curtipes* as well). **Lynch** (1984) revised his *myersi* series (or group) and separated the species into three components, one for *ginesi* and *nicefori*, one for *orestes* and *vidua*, and a third for *myersi*, *ocreatus*, and *trepidotus*. The last three species were assigned to the *pyrrhomerus* group.

Based on a review of the literature, it is not unreasonable to presume that *E. ginesi* and *E. nicefori* might be closely related. Although each was contrasted with *E. curtipes*, they have never been contrasted with one another.

Materials and Methods

Specimens were measured to the nearest 0.1 mm using dial calipers under a dissecting microscope. Sex was determined using gonadal examination which also allows some measure of relative age (especially for females). In the accounts below, means are reported as \pm one standard error of the mean.

Taxonomic Accounts

Eleutherodactylus ginesi, *E. nicefori*, and the frog from the Alto del Tigre are distinct species in spite of

the similarities evident in descriptions. The undescribed species from Alto del Tigre appears to be the nearest relative of *E. nicefori* for which I offer the name,

Eleutherodactylus nervicus sp. nov.

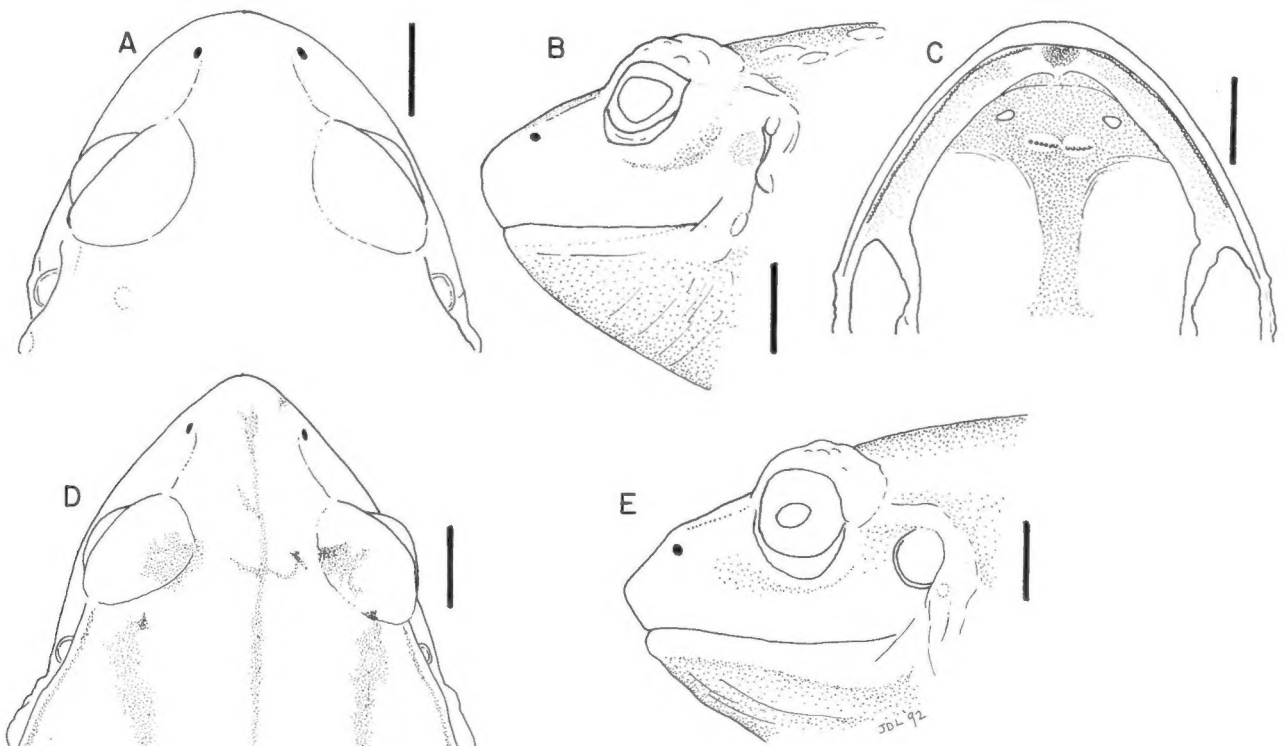
Holotype. ICNMHN 32323, an adult female, one of a series collected on 5 march 1987 by *M.C. Ardila*, *J. E. Hurtado* and *S. Tello*.

Type-locality. Alto del Tigre, límite Cundinamarca-Meta, carretera Guayabetal-El Calvario, Colombia, 3870 m.

Paratopotypes. ICNMHN 26948, 32313-21, 32322 (cleared and stained skeleton), 32324-32.

Diagnosis. (1) skin of dorsum bearing numerous small warts, short ill-defined dorsolateral folds, that of venter areolate; (2) tympanum visible, superficial, round, its diameter 33.3-51.8% eye length; (3) snout subacuminate in dorsal view, pointed in lateral profile; canthus rostralis sharp, concave; (4) upper eyelid narrower than IOD; no cranial crests; (5) vomerine odontophores low; (6) males with vocal slits, subgular vocal sac; no nuptial pads; (7) first finger slightly shorter than second; digits bearing narrow discs; (8) lateral keels on fingers; (9) no ulnar tubercles; (10) no tubercles on heel or outer edge of tarsus; elongate tubercle on inner edge of tarsus; (11) two metatarsal tubercles, inner oval, 3-4 times size of round outer; supernumerary plantar tubercles present; (12) toes bearing lateral fringes, no webbing; toe discs narrow; V longer than III; (13) dorsum gray to reddish-brown with brown stripes; venter cream with faint to dense reticulum of brown; (14) adults small,

Figure 1. *Eleutherodactylus nicefori* (A) top of head, ICNMHN 10432; (B) side of head, ICNMHN 10257; (C) palate, ICNMHN 22304; and *E. nervicus* (D) top of head, ICNMHN 32326; (E) side of head, ICNMHN 32325. Scales equal 2 mm.



males 15.8-18.5 ($\bar{x} = 16.8 \pm 0.3$, $n = 9$) mm SVL, females 23.9-26.0 ($\bar{x} = 24.5 \pm 0.3$, $n = 6$) mm SVL.

Eleutherodactylus nervicus shares its narrow digital discs with several species (see Lynch, 1984) but differs from *E. ginesi* and *E. nicefori* in having complete circumferential grooves surrounding the ventral pads of the discs. Furthermore, *E. nervicus* has vocal slits and a pointed snout unlike *E. ginesi*. The pointed snout of *E. nervicus* also serves to distinguish it from *E. nicefori*.

Description (proportions based on nine males and nine adult and young females). Head almost as wide as body in males, narrower than body in adult females, wider than long; HW 38.3-43.5 ($\bar{x} = 40.7 \pm 0.6$)% SVL in males, 37.2-43.4 ($\bar{x} = 40.2 \pm 0.6$)% in females; snout subacuminate in dorsal view, pointed in lateral profile (Fig. 1); nostrils protuberant, directed laterally; E-N 66.7-85.0 ($\bar{x} = 73.8 \pm 1.7$)% eye length in males, 75.0-88.0 ($\bar{x} = 79.7 \pm 1.3$)% in females; canthus rostralis sharp, concave; loreal region concave, sloping abruptly to lips; lips not flared; low, rounded tubercles on upper eyelid; interorbital space flat, no cranial crests; upper eyelid width 59.1-70.8 ($\bar{x} = 65.2 \pm 1.5$)% IOD in males, 51.5-66.7 ($\bar{x} = 59.0 \pm 1.7$)% in females; supratympanic fold thick, extending to above insertion of arm; tympanum round, superficial, annulus distinct, separated from eye by distance equal twice its length; postrictal tubercles not conical; tympanum length 38.1-47.6 ($\bar{x} = 42.0 \pm 1.1$)% eye length in males, 33.3-51.8 ($\bar{x} = 42.3 \pm 1.7$)% in females; choanae small, round, not concealed by palatal shelf of maxillary arch; vomerine odontophores

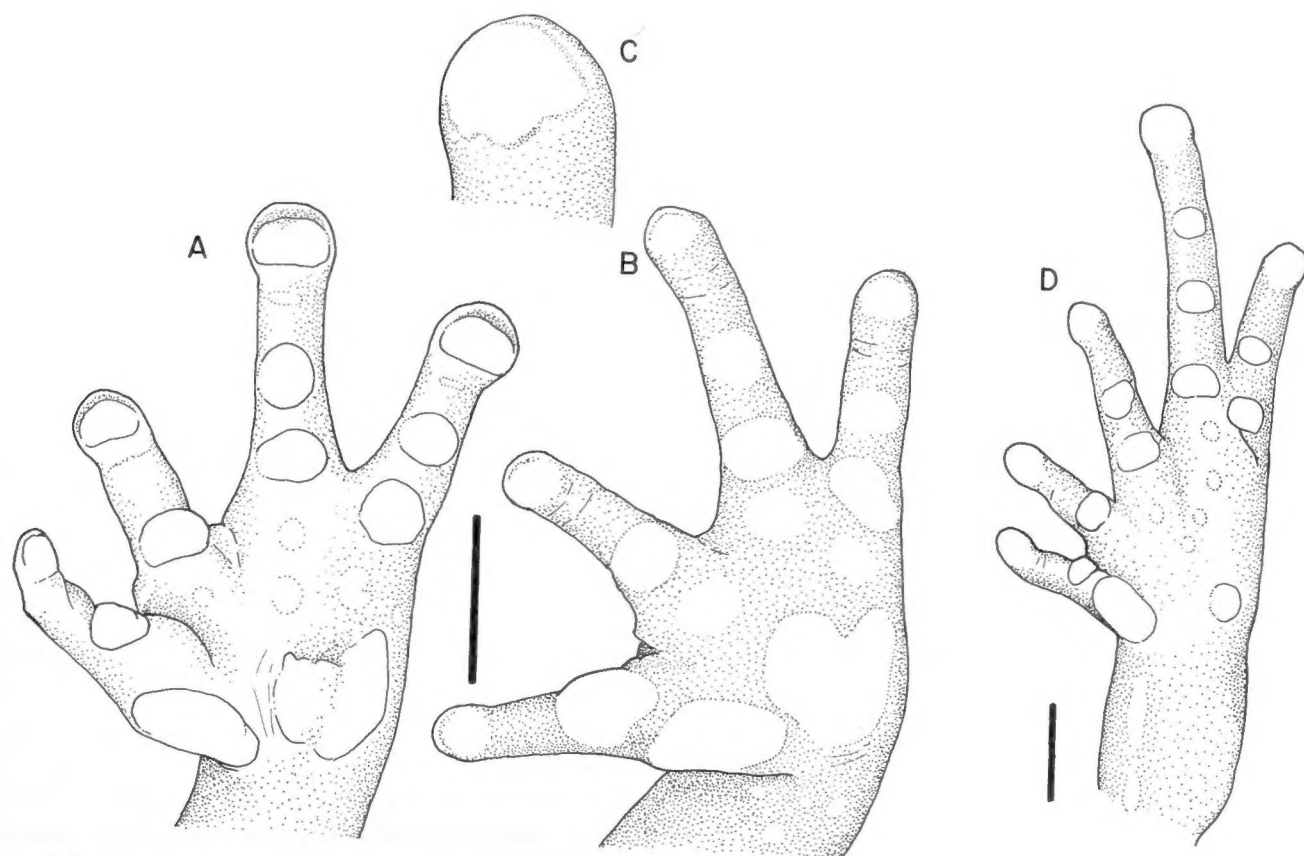
median and posterior to choanae, oval, low, ill-defined, bearing a few pungent teeth; tongue longer than wide, posterior border notched, posterior 2/5 not adherent to floor of mouth; vocal sac single, subgular; short vocal slits posterolateral to tongue.

Skin bearing many small warts becoming more coarse on flanks; short postocular folds; short dorsolateral folds from scapular to sacrum regions; another indistinct fold lateral to that one, appearing as a series of fused warts; discoidal folds anterior to groin; venter and undersides of thighs areolate, throat more finely granular.

No ulnar tubercles; palmar tubercle bifid, larger than oval thenar tubercle; supernumerary palmar tubercles numerous, low; subarticular tubercles round, non-conical; digits short with narrow discs (Fig. 2) bearing ventral pads (broader than long), completely defined by circumferential grooves; first finger slightly shorter than second; fingers bearing lateral keels; thumbs of males swollen but without nuptial pads.

No tubercles on heel or outer edge of tarsus; elongate inner tarsal tubercle about one length of inner metatarsal tubercle proximal to metatarsal tubercle; inner metatarsal tubercle oval, 3-4 times size of round outer metatarsal tubercle; prominent supernumerary plantar tubercles at bases of toes I-IV, less obvious tubercles proximal to these; subarticular tubercles round, low; toes with lateral fringes but no webbing; toes with discs, discs slightly wider than digit below pad, and pads (pads

Figure 2. (A) *Eleutherodactylus nervicus*, ICNMHN 32324; (B) *E. nicefori*, ICNMHN 22314; (C) tip of third finger of ICNMHN 22314, X4; (D) plantar view of foot of *E. nicefori*, ICNMHN 20946. Scales equal 2 mm.



defined by complete circumferential grooves); third toe shorter than fifth when each adpressed against IV (tip of third toe reaches to penultimate subarticular tubercle of toe IV, tip of fifth toe reaches to distal half of distal subarticular tubercle of toe IV); toe V fused to IV to base of distal subarticular tubercle of V; heels not touching when flexed hind limbs held perpendicular to sagittal plane; shank 39.3-42.5 ($\bar{x} = 41.2 \pm 0.4$)% SVL in males, 39.9-45.2 ($\bar{x} = 41.4 \pm 0.6$)% in females.

Dorsum gray to tan to reddish-brown with converging dark lines from eyes to center of back where lines diverge into diffuse spots; some dark spots, infuscation, or 2-3 narrow slanted lines on flanks; brown canthal-supratympanic stripe; labial bars vague but no cream stripe on upper lip; face and side of head darker than dorsum; posterior surfaces of thighs either uniformly stippled with brown or bearing small pale flecks on slightly darker field (toward knee); no anal triangle; limb bars narrower than interspaces, frequently incomplete; venter cream with faint brown stippling to a dense loose reticulum of gray or brown (forming cream spots in ICNMHN 32324); throat less heavily pigmented than venter; undersides of limbs pigmented only in darkest individuals.

Etymology. Latin, meaning nervous, in allusion to the riding on the back of the tiger. Coincidentally, Alto del Tigre is a local focus of the guerilla group "FARC" and the "road" leading to the top is very narrow and hangs precariously upon ridges and the side of the mountain, leading the collectors to be nervous as well as they ascended the back of the tiger.

Natural history. *E. nervicus* was collected only once during a hurried visit to the TV tower at the peak of Alto del Tigre. Nevertheless, a single female (ICNMHN 26948) was found guarding a clutch of recently deposited embryos beneath a rock. Among the series of 20 individuals collected is a single juvenile male (ICNMHN 32332), 12.4 mm SVL, who lacks vocal slits. The male has large white testes as do adult males. One juvenile female (ICNMHN 32331), 16.0 mm SVL, has straight, narrow oviducts. A slightly larger female (ICNMHN 18.8 mm SVL) has indications of bends in her oviducts. Yet larger females (21.9-22.6 mm SVL) are classified as young because their oviducts show narrow convolutions for the length of the tube. This range of reproductive status among a small sample is consistent with an aseasonal pattern of reproduction. All individuals were found beneath stones and debris during the day, suggesting that the species is nocturnal.

Eleutherodactylus nervicus exhibits the "S" condition of the adductor muscles of the jaw (Lynch 1986) and the *SQat* condition of the *m. depressor mandibulae* (Lynch, 1993). It does not have an exposed frontoparietal fontanelle and differs from *E. ginesi* which does have an exposed fontanelle (Rivero, 1984, *contra* Lynch, 1968).

Eleutherodactylus nervicus may well be restricted in distribution to Alto del Tigre. Previous efforts to collect this mountain were unsuccessful in reaching the peak

and produced good series of *E. affinis* (Werner) at lower (ca. 3200 m) elevations in forested habitats. Collecting over the past decade in the mountains to the east of Bogotá (at elevations between 3100 and 3600 m) has yielded *E. affinis*, *E. bogotensis* (Peters), and *E. elegans* (Peters) but not *E. nervicus* in páramo habitats.

Eleutherodactylus nicefori Cochran & Goin

Although described by Cochran and Goin (1970), *E. nicefori* is poorly known. Little literature has accumulated on the species and many of the comments included in that limited literature contain errors. To correct some of those errors, I here provide a diagnosis and redescription of the species.

Diagnosis. (1) top of head and anterior dorsum relatively smooth, other dorsal surfaces bearing flat warts, sometimes fusing into loose folds in dorsolateral region, throat and venter coarsely areolate; (2) tympanum round, partially concealed by thick supratympanic fold in some populations (Almorzadero, El Empalme), concealed beneath skin in others, when exposed, superficial, round; its length 30.0-52.4% eye length in all populations; (3) snout acuminate in dorsal view in males, rounded in adult females, rounded in lateral profile in all; canthus rostralis relatively distinct, concave; (4) upper eyelid narrower than IOD, no cranial crests; (5) vomerine odontophores prominent, oval, juxtaposed, bearing transverse rows of teeth; (6) males with short vocal slits posterolateral to tongue, small, subgular vocal sac; thumbs swollen in breeding males, no nuptial pads; (7) first and second fingers subequal in length; digits not expanded into discs, indistinct terminal grooves present; (8) vague lateral keels on fingers; (9) no ulnar tubercles; (10) no heel or tarsal tubercles; indistinct thickened fold on distal 1/4 of inner edge of tarsus; (11) two metatarsal tubercles, inner oval, ca three times size of round outer; indistinct supernumerary plantar tubercles at bases of toes II-IV; (12) toes bear vague lateral keels, no webbing; toes lack discs, circumferential grooves poorly defined or absent; when toes III and V are adpressed against IV, toe V longer than toe III; (13) dorsum tan to pale brown to reddish-brown with dark (brown or black) spots and/or slanted bars on flanks; some have dark blotches on dorsum as well; black interorbital bar, canthal-supratympanic stripes; labial "bars" represented by dark brown spots below eye, not reaching lip; upper lip cream to pale brown; limb bars rarely complete, when complete as wide as interspaces; posterior surfaces of thighs cream with scattered brown spots; throat and venter cream without dark markings or venter bearing small brown/black spots; in some populations, venter darker and more heavily spotted (occasional individuals have nearly black venters with white spots, e.g., Mpio. Güican, Boyacá); (14) adults small, males 13.6-23.5 ($\bar{x} = 18.7$, $n = 126$) mm, females 19.8-30.8 ($\bar{x} = 25.8$, $n = 168$) mm SVL; some geographic variation in size (see below).

Description. Head not as broad as body, wider than long; HW of males 35.4-41.4 ($\bar{x} = 38.2 \pm 0.2$, $n = 26$)% SVL, of females 35.8-41.0 ($\bar{x} = 38.3 \pm 0.2$, $n = 34$)%; snout subacuminate in males (although usually rounded in the Páramo del Almorzadero population) and young

females, rounded to obtuse in adult females, rounded in lateral profile; nostrils not, or only weakly, protuberant, directed dorsolaterally; E-N of males 62.5-90.0 (\bar{x} = 78.1 \pm 1.6, n = 26)% eye length, of females 74.1-96.0 (\bar{x} = 84.6 \pm 1.0, n = 34)%; canthus rostralis evident, rounded, gently concave; loreal region concave, sloping abruptly to lips; lips not flared; low tubercles on posterior part of upper eyelid, none pungent or prominent; no cranial crests, interorbital space flat; upper eyelid width of males 61.5-80.8 (\bar{x} = 70.2 \pm 0.9, n = 26)% IOD, of females 59.4-87.0 (\bar{x} = 68.5 \pm 1.1, n = 34)%; supratympanic fold thick, ending above insertion of upper arm amidst large flat tubercles, obscuring posterodorsal part of tympanum, if visible; tympanum concealed beneath skin in some populations, in others lower part of annulus distinct, round, separated from eye by distance equal 1 1/2 - 2 times its length; tympanum of males 35.0-52.4 (\bar{x} = 44.1 \pm 1.4, n = 15)% eye length, of females 33.3-48.2 (\bar{x} = 44.6 \pm 0.7, n = 25)%; postrictal tubercles not conical; choanae moderate-sized, round, not concealed by palatal shelf of maxillary arch; vomerine odontophores median and posterior to choanae, each larger than a choana, oval, juxtaposed (Fig. 1), bearing 5-6 teeth in arched rows; tongue slightly longer than wide, posterior 2/5 - 1/2 not adherent to floor of mouth, posterior border with slight indications of notch; vocal slits short, extending from angle of jaw one-half way to base of tongue, far back in throat and easily overlooked; vocal sac subgular, median.

Skin of head smooth, that of dorsum finely granular, becoming more coarse on flanks; indistinct folds present — postocular folds, dorsolateral pair, another pair slightly lower on flanks (sometimes appearing as a series of fused warts); throat and venter areolate; discoidal fold anterior to groin; undersides of thighs areolate; anal opening not extended in sheath.

No ulnar tubercles or folds; palmar tubercle bifid (outer lobe nearly separated from medial), about twice size of oval thenar tubercle; supernumerary palmar tubercles large, indistinct; subarticular tubercles broader than long, rounded; lateral keels of fingers ill-defined; fingers lacking discs, tips only slightly wider than digits, circumferential grooves weakly evident at tips or absent (Fig. 2); first finger shorter than second; thumb of sexually active males swollen but no nuptial pad.

No tubercles on heel or along outer edge of tarsus; thickened ridge along distal 1/4 - 1/2 of inner edge of tarsus; inner metatarsal tubercle oval, outer round, 1/3 - 1/2 size of inner; plantar supernumerary tubercles ill-defined; subarticular tubercles round to slightly wider than long, not conical; lateral keels on toes coalescing at bases of digits but "web" not encompassing basal subarticular tubercles except between IV and V; toe V joined to IV almost to base of distal subarticular tubercle of V (Fig. 2); when toes III and V are adpressed against IV, V longer than III; toe tips swollen but not expanded into discs; traces of circumferential grooves at tips of most toes; heels not touching when flexed hind limbs held perpendicular to sagittal plane; shank of males 30.9-38.6 (\bar{x} = 34.3 \pm 0.4, n = 26)% SVL, of females 31.5-37.5 (\bar{x} = 33.8 \pm 0.2, n = 34)%.

Top of head and back tan to reddish-brown (sometimes with pale cream or tan blotches above occiput and sacrum) and bearing small black spots, sometimes forming loose Y-shaped marks above vertebrae; black slanted bars on flanks, tending to fuse and form distinct line in dorsolateral region (this pattern is most pronounced in the dorsoconcolor morph where dorsum is uniform reddish-brown and flanks are black with slanted tan lines); brown or black canthal-supratympanic stripe; edge of upper lip cream; only occasionally are traces of labial bars evident (e.g., ICNMNH20994); limb bars rarely complete, transverse, slightly narrower than interspaces; posterior surfaces of thighs cream with brown or black spotting; no anal triangle; ventral surfaces vary from creamy-white with no markings through scattered dark flecks across abdomen to heavy black spotting/reticulation over venter and specks on throat to black venter with cream reticulum and cream throat speckled with black; undersides of limbs feebly speckled but in those with darkest venters, undersides of limbs pale brown with traces of cream spots.

Eleutherodactylus nicefori, like many other species of the genus is pattern polymorphic (Fig. 3). The **Raphe** pattern consists of a broad stripe of pale pigment down the center of the back which disrupts the underlying pattern of blotches. Some darker pigment at the edges of the vertebral raphe serves to make the raphe more distinct. The **Hairline** pattern is similar except that the pale vertebral stripe is very narrow. In this pattern, there often is a hairline of pale pigment on the venter as well but thin pale lines do not run along the posterior surfaces of the thighs and undersides of shank and tarsus or across the breast and along the undersides of the arms as in some other species of *Eleutherodactylus* (e.g., *E. ginesi*, Rivero, 1984, *E. ocreatus*, Lynch, 1981a). The **Dorsoconcolor** pattern consists of a uniform dorsal surface (cream to reddish-brown), defined laterally by dark (usually black) pigment. The lateral margins of the pale dorsum are straight and well-defined.

In addition to these three morphs, I have recognized three others which are probably not discrete morphs but rather represents modes from a continuum of individual variation. The **Pale Blotches** pattern consists of two pale blotches, outlined in darker pigment, one over the sacral region and the second over the occiput or scapular region. This pattern usually occurs with what I call below the **Spotted** pattern. The **Spotted** pattern is that described above as the "normal" color pattern for *E. nicefori*. The spots vary in intensity, with those found on the upper flanks being, in general, the darkest. Individuals show a broad range of completeness to the spotted pattern, ranging from well spotted to a pattern of only a few small spots (Fig. 3D-F). The **Plain** pattern is probably nothing more than the most reduced variant of the spotted pattern.

Although Rivero (1984) reported that *E. nicefori* lacks vocal slits and Cochran and Goin's (1970) account is ambiguous (they did not determine sexes of their individuals), *E. nicefori* males have short vocal slits. The vocal sac is not paired as reported by Cochran and Goin (1970). Males have very large white testes that fill the abdominal cavity (Fig. 4). Vocal slits and large testes

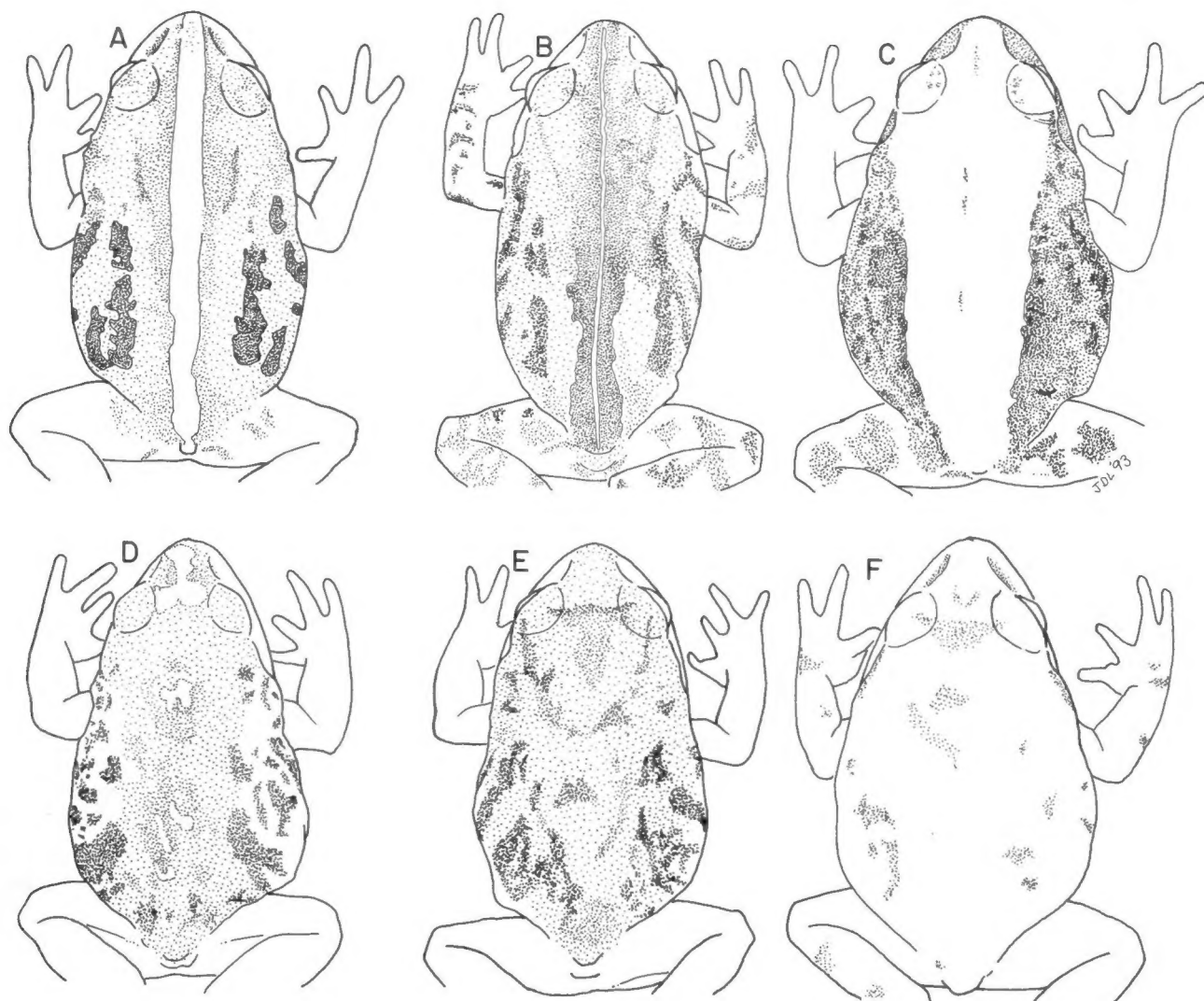


Figure 3. Pattern polymorphism in *Eleutherodactylus nicefori*. (A) raphe, ICNMHN 20906; (B) thin middorsal line, ICNMHN 21021; (C) dorsoconcolor, ICNMHN 20826; (D) pale blotches, ICNMHN 21028; (E) spotted, ICNMHN 21042; (F) reduced spotting, ICNMHN 20921.

were found in nearly every male examined but occasional males (small individuals) were found that lacked vocal slits and did not have swollen thumbs. These are treated here as juvenile males.

Natural history. Most of the specimens known of this species were collected by *María Cristina Ardila* and *Pedro M. Ruiz* in páramo habitats during the day. They report in their field notes that the frogs were inactive, being found beneath rocks and fallen *Espeletia* trunks. Their failure to note vocalizations I attribute to their failure to collect during the night. Amplectant pairs (including a pair of males) were found beneath rocks or trunks during the day as well. One female was found guarding a freshly deposited clutch of eggs.

The sizes of amplectant pairs provide an opportunity to "test" the mean sizes of adults calculated from collections of isolated males and females. ICNMHN 5030-31 were an amplectant pair collected in the Páramo de Pisba (Socotá). The male is 18.5 mm and the female is 29.1 mm SVL. ICNMHN 20833 and 22281 were an amplectant pair collected on the slopes of Nevado del Cocuy (Güicán); he is 16.0 mm and she is 26.3 mm SVL.

At the same locality, another amplectant "pair" was found (ICNMHN 20834-35) but each of these is a mature male, 17.1 and 18.1 mm SVL, respectively.

Although the samples of males from northern populations are small, the animals from Chitagá and Tona appear to be smaller than those from more southern localities. Males from populations on the slopes of Nevado del Cocuy (Chiscas, Cocuy, and Güicán) are larger than males from other populations. Those from the Páramo de Pisba (Chita and Socotá) are only slightly larger than those from the northern populations. This pattern is not matched by females except that the largest females come from Chiscas. Using the largest juvenile female (thin oviducts with no evidence of convolutions, only small ovarian eggs) as the metric, the pattern seen in males is repeated (Table 1). However, the variability seen among pre-mature or young females (oviduct showing some bending, eggs small) obscures the pattern. The smallest mature female found (19.8 mm SVL) comes from a northern population (Chitagá) but the second smallest one found (20.8 mm SVL) comes from a central population (Cocuy).

Distribution. Páramo and subpáramo habitats (2770-4100 m) on the easternmost range of the Cordillera Oriental in northern Depto. Boyacá and southern departamentos Norte de Santander and Santander.

Remarks. *Eleutherodactylus nicefori*'s simple digit tips (Fig. 2) are more simple than seen in nearly all *Eleutherodactylus* and approach closely the condition(s) of the frogs assigned to the genus *Phrynopus* (Cannatella, 1984; Lynch, 1975). Several species of *Eleutherodactylus* lack disks (= have no expansion of the digit tip) but nearly all of the narrow-toed species have circumferential grooves defining the ventral pad. Pads (and circumferential grooves) are absent on the hands of some species but present on the feet (Lynch, 1981b) or are absent on some (inner) digits (Lynch, 1980, 1989) but in each case there are some digits exhibiting pads. In *E. nicefori*, the pads are very difficult to detect, even under high magnification (Fig. 2) and I am not confident that the objects detected are homologous with the pads seen in other *Eleutherodactylus*. The terminal phalanges do show evidence of being T-shaped (Fig. 5), with the best development of the lateral projections being seen on the foot; the terminal phalanx of the thumb does not bear lateral projections.

For those seeking evidence that *Phrynopus* are simply *Eleutherodactylus* having greatly reduced digit tips, *E. nicefori* offers such evidence. However, at present it seems premature to combine *Phrynopus* with *Eleutherodactylus*. The Colombian *Phrynopus* are under

study by my colleagues *M. Ardila* and *P. Ruiz* and include several species, not the single species mentioned by Lynch (1975). Until the other species are described, it is preferable to retain *Phrynopus* as a device to hold the eleutherodactyline frogs with reduced digits.

The structural simplicity of the digits of *E. nicefori* is equalled by the digits of a Venezuelan species, *E. ginesi*, monographed by Rivero (1984). Rivero (1984) did not consider *E. ginesi* closely related to *E. nicefori* (as did Lynch, 1981a) but rather with Ecuadorian species.

Specimens examined. (613) BOYACÁ: ICNMHN 20807-11 (C&S). *Mpio. Chiscas*: cabeceras Caño Ruconcito, Km 17 carr. Chiscas-Las Cañas, 3580 m, ICNMHN 21090-146; Km 16 carr. Chiscas-Las Cañas, Siachoque, 3600 m, ICNMHN 20931-51; Páramo Alto Siachoque, 3950-3980 m, ICNMHN 20982-21000. *Mpio. Chita*: Km 11-12 carr. Chita-El Empalme, 3370-3420 m, ICNMHN 20905-09, 20911-13, 20915-29; carr. Chita-La Salina, vereda El Arbolito, Páramo de Pisba, 3400 m, ICNMHN 3579-3610, 3961-67; Km 2 carr. El Empalme-Socha, 3480 m, ICNMHN 20875-76, 20878-82, 20884, 20886-88; vereda La Lajita (Parpa), Km 79-80 carr. Socha-Sácama, flanco oriental Páramo de Pisba, 3420 m, ICNMHN 5823, 5832, 5844-45, 5952, 5959-74. *Mpio. Cocuy*: vereda La Capilla, Km 7 carr. La Capilla-El Cocuy, 3690 m, ICNMHN 20889-904; Páramo Alto Mahoma, 3800 m, ICNMHN 21041-87, 3900 m, ICNMHN 21001-40. *Mpio. Güican*: Sierra Nevada del Cocuy, Hda. Ritacua, \pm 3500 m, ICNMHN 5101-02, arri-

Figure 4. Drawings of dissection of *Eleutherodactylus nicefori* showing size and position of testes. Uncatalogued male from collection made in Municipio Güican, Boyaca. (A) lateral view, viscera except testes removed; (B) same in ventral view; (C) ventral view, liver removed; (D) ventral view prior to removal of organs. Scale equals 3 mm.

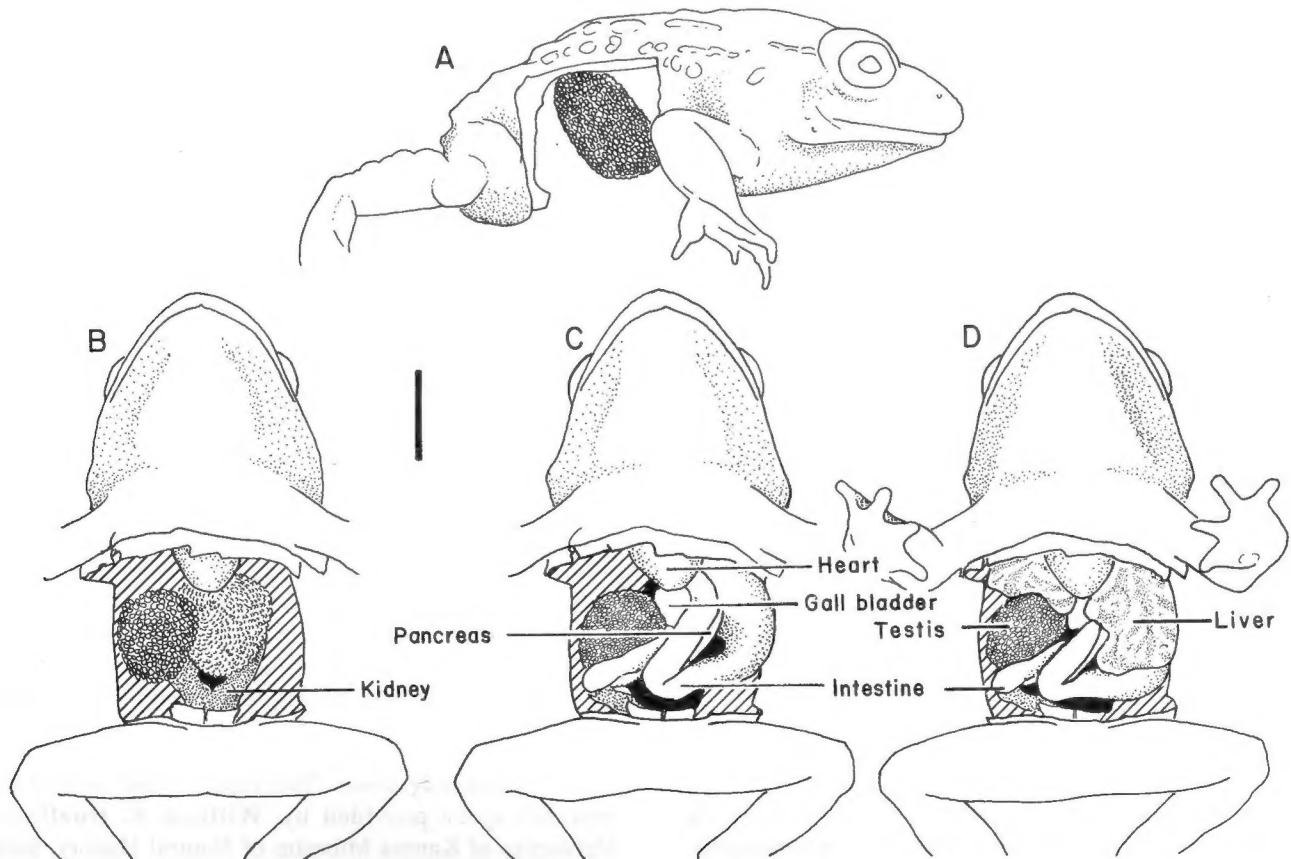


TABLE 1. POPULATION VARIATION IN SIZE (SVL) OF FEMALES OF *ELEUTHERODACTYLUS NICEFORI* (IN MM).

Locality	JUVS	YOUNG	ADULTS	(N)	MEAN \pm 1 S.E.
Tona	-17.4	22.6-24.2	23.2-29.0	(11)	26.1 \pm 0.5
Chitagá	-17.9	17.8-21.4	19.8-27.9	(27)	24.6 \pm 0.4
Chiscas	-22.0	20.3-26.1	23.3-30.8	(29)	27.2 \pm 0.3
Güicán	-20.6	19.1-24.2	21.8-29.2	(35)	25.5 \pm 0.3
Cocuy	-21.8	20.8-21.3	20.8-27.6	(23)	25.1 \pm 0.4
Chita	-20.9	20.5-25.2	24.5-30.0	(26)	26.7 \pm 0.3
Socotá	17.9	20.5-23.0	22.9-28.1	(5)	25.6

ba de [Hda] la Esperanza, \pm 3500 m, ICNMHN 4054, Alto de Ritacueva, 3300-4100 m, ICNMHN 10253-72, Alto de Ritacueva, via a Laguna de los Verdes, 3920 m, ICNMHN 10273-79; vereda El Tabor, Cabañas Corturismo, 3920 m, ICNMHN 20821-22, 20870-74, 22333, 22335-46, Páramo El Verde, finca Las Playitas, 3850 m, ICNMHN 20826-32, 22260, 22263-80, camino a la Sierra, Pico Ritacueva Blanca, finca Las Playitas, 3850-3920 m, ICNMHN 20833-55, 22281-97; vereda Pantanillo, 4180 m, ICNMHN 6280-87; vereda [San Antonio de] la Cueva, El Alto, Km 5, carr. Capilla-El Cocuy, 3900 m, ICNMHN 20856-69, 22298-304, 22306-31, Hacienda La Esperanza, 3500 m, ICNMHN 2614-16, La Esperanza, Caño Rancho Quemado, Páramo Lagunillas, 3850-3950 m, ICNMHN 20952-81. *Mpio. Socotá*: vereda La Lajita (Parpa), Km 60-68 carr. Socha-Sácama, flanco occidental Páramo de Pisba, 3400-3590 m, ICNMHN 5819, 5821 (C&S), 5830, 5831 (C&S), 5927-36, 5938. NORTE DE SANTANDER. *Mpio. Chitagá*: "Chitagá, Santander" (correct locality data almost certainly = Páramo del Almorzadero, hacia Chitagá, exchanged from MLS), KU 150710-13; 18.5 km S Chitagá, 2850 m, KU 168445-80, 170144-46 (C&S); 32 km S Chitagá, 3400 m, KU 168481-516; Km 34 carr. Chitagá-Málaga, 3320 m, ICNMHN 10403-04; Páramo del Almorzadero, KU 150715-24, MLS 25 (2), 30 (2), USNM 147013; Páramo del Almorzadero, Km 37 carr. Chitagá-Málaga, 3430 m, ICNMHN 10411-31, Km 43-44 carr. Chitagá-Málaga, 3670-3740 m, ICNMHN 10432-47; vereda Piedras, sitio Vegas de Colombia, 2770 m, ICNMHN 10402. SANTANDER. *Mpio. Tona*: Páramo de Berlín, Km 49 carr. Bucaramanga-Pamplona, 3400 m, ICNMHN 10375-401.

Discussion

With the description of *E. nervicus*, 20 dwarf *Eleutherodactylus* have been described from the Andes of northwestern South America (Colombia, Ecuador, and Venezuela). Two of these are from Venezuela (*E. boconoensis* and *E. ginesi*), two occur in the Cordillera Oriental of Colombia (*E. nervicus* and *E. nicefori*), five in the Cordillera Central (*E. leptolophus*, *E. maculosus*, *E. peraticus*, *E. scoloblepharis*, and *E. uranobates*), and eleven are found in Andean Ecuador and extreme southern Colombia. Lynch (1991) proposed grouping the five species from the Cordillera Central as the *leptolophus* group because these species have relatively large digital

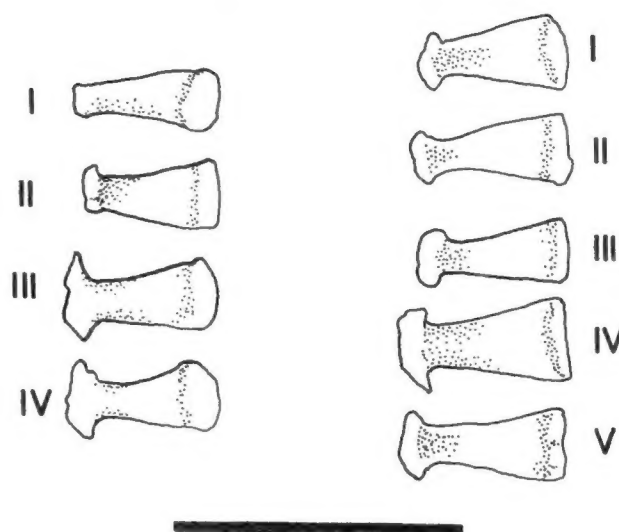


Figure 5. Plantar views of terminal phalanges of right hand (left, digits numbered I-IV) and right foot (digits numbered I-V) of *Eleutherodactylus nicefori*, ICNMHN 5821.

disks in contrast to the other species which show little or no expansion of the digit tips. The species of the *leptolophus* group also share another character in which when the third and fifth toes are adpressed against the fourth, the fifth toe is much longer than the third (= tip of toe V reaches distal border of distal subarticular tubercle of toe IV whereas tip of toe III reaches no more than distal border of penultimate subarticular tubercle of toe IV). In *E. nervicus*, one finds an identical condition. In *E. nicefori*, the fifth toe is only slightly shorter, reaching to the middle of the distal subarticular tubercle of toe IV. This condition is also seen in the slightly larger (La Marca and Smith, 1982) Venezuelan *E. colostichos*.

In contrast, the remaining dwarf species exhibit a condition in which the tip of the fifth toe does not extend beyond the tip of the third (*E. ginesi*, *E. myersi*, *E. ocreatus*, and *E. trepidotus*) or only slightly extends beyond the tip of toe III. In these frogs, the tip of toe V reaches no more than to the distal border of the penultimate subarticular tubercle of toe IV. This is the plesiomorphic condition in *Eleutherodactylus* and is found in all other leptodactylids.

Although here united by a plesiomorphic (=uninformative) feature, I include the following species in the *myersi* group of *Eleutherodactylus*: *boconoensis* Rivero & Mayorga, *gladiator* Lynch, *ginesi* Rivero, *hectus* Lynch & Burrowes, *leoni* Lynch, *myersi* Cochran & Goin, *ocreatus* Lynch, *orestes* Lynch, *pyrrhomerus* Lynch, *repens* Lynch, *simonbolivari* Wiens & Coloma, *trepidotus* Lynch, and *vidua* Lynch. The two Venezuelan species (*boconoensis* and *ginesi*) appear to be closely allied to one another and to another undescribed species under study by Enrique La Marca and may not be allied closely to the eleven species from southern Colombia and Ecuador.

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